ON THE MECHANICAL GENESIS OF THE SCALES OF FISHES.

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Fourteen years ago the present writer suggested that the slow metamorphosis of the forms of the crowns of the teeth of mammalia,[1] in the course of a vast number of successive generations, might be ascribed to the continuous, slow and cumulative action of mechanical strains and pressures in definite directions, resulting in the production of permanent stresses and consequent changes in the forms of the crowns, especially of the molar series. The evidence since accumulated from vertebrate palæontology and anatomy has served to strengthen the belief that such an hypothesis cannot be dismissed as useless until a better one has been offered in its stead. The present paper is an attempt to apply somewhat analogous reasoning to a somewhat simpler, but no less interesting, problem in morphogenesis.

The mechanical hypothesis now to be offered respecting the genesis of the scales of fishes, accounts for the origin of such scales from a continuous subepidermal matrix, which may be regarded as a basement membrane. Such a matrix is found to actually exist in some forms, at an early stage, just beneath the epidermis. It is thickest on the dorsal and lateral aspects of the body as is seen in sections of the young of the scaleless *Batrachus tau*, for example. Such a matrix also exists in the larval stages of other scale-bearing forms and may be continuous with the very attenuated basement membrane from which the actinotrichia or primordial fin-rays of embryo fishes seem to be in part differentiated. Such a matrix is almost co-extensive with the whole epidermal layer of the young of many types of fishes, just at the time when the scales commence to be developed.

The hypothesis further accounts for the arrangement of the scales in longitudinal and in oblique rows in two directions. The oblique rows are arranged, as is well-known, in a direction from above downward and backward and also in the reverse direction from below upward and backward. That is, the scales may be counted in rows in three directions downward and forward as well as down-

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[1] On the Mechanical Genesis of Tooth-forms. Proc. Acad. Nat. Sciences, 1878.

ward and backward, and, starting from any scale in any oblique row, they may be counted either forward or backward longitudinally or in conformity with the direction of the axis of the body of the fish. This is conspicuously the case in Clupeoids and some Cyprinoids.

In such archaic types as these, approximating the primitive iso-spondylous condition, it is also found that the number of scales in a longitudinal row corresponds, on the sides of the body, very exactly with the number of muscle-plates or somites of the body. It is also found that the myocommata or sheets of connective tissue interven-ing between the successive somites are attached with great firmness to the deeper layers of the skin or corium. Such a construction, together with the peculiar arrangement of the muscle plates at the time the scales begin to develop conditions the further growth of the scale matrix. This is affected in such a manner that the whole of the integument is thrown into definitely circumscribed areolæ, during the ordinary movements of the fish in swimming. The central portions of each of these areolæ are left in a quiescent con-dition while their margins are wrinkled or folded as a result of the current action of the lateral muscles of the body. In this wise each and every one of the dermal and epidermal areolæ are circum-scribed by the action of the fish in the normal act of swimming. In each of the circumscribed areolæ a scale develops; the continuity of its development with its fellows across the margins of the areola is prevented by the continual bendings or flexures to which the dermis is there subjected owing to the action of the muscles.

This will be better understood by referring to the accompanying diagram representing the arrangement of the muscular somites of a Cyprinoid (*Carassius*) with their intervening myocommata as seen from the side when the skin with its scales is removed. Before proceeding further, however, it may be well to insist upon the fact that the rows of scales are found to conform to the successive somites. This is of itself significant. The careful interpretation of the facts from observation, however, discloses a very remarkable effect due to the peculiar arrangement of the muscle plates.

As is well known the muscular masses of the sides of the body of a fish are arranged in the form of two longitudinal trihedral columns separated along the middle line of the side a to b into a dorsal and ventral half. The somites entering into the composition of these ventral and dorsal masses were at first absolutely continuous across

the longitudinal, horizontal septum a, b. If we suppose the somites of the adult as developed from a continuous embryonic segment
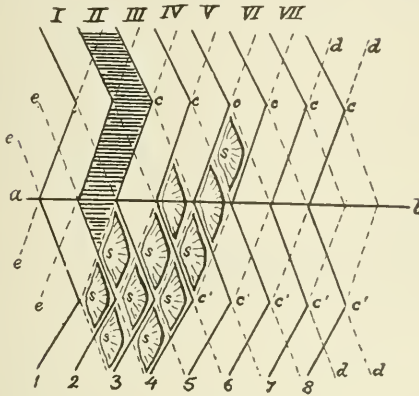

FIG. I.

extending the whole depth of the body, then will somites I, II, III, IV, V etc., in the figure form two parallel series of m u s c u l a r blocks above and below the line a, b. Each half somite is also seen to present an acute apex directed backward at the points c and c' above and below the line a, b. The somites I, II, III, IV and V are therefore sigmoid in outline as seen from the exterior. The myocommata or connective tissue septa 1, 2, 3, 4, 5, 6 etc., which intervene between the somites, have a corresponding sigmoid arrangement. The sigmoid or ⪦-shaped myocommata and the myotomes, are reciprocally coadapted to each other in configuration like a nest of ⪦ ⪦ ⪦ ⪦'s turned upon their sides. If we further supposed that thin and thick-legged ⪦'s alternated thus ⪦ ⪦ ⪦ ⪦ ⪦ ⪦ we might suppose the thin-legged ones to represent the myocommata and the thick-legged ones the muscle plates or myotomes. The muscular fibres of the thick-legged ⪦'s run longitudinally from the posterior surface of the myocomma immediately in front of it, to be inserted into the anterior face of the myocomma immediately behind it. The muscular tension is therefore exerted upon the opposite sides of the myocommata and is thus propagated along the sides of the body from the head to the tail, from the first to the last myotome. But the tension upon the inner face of the skin is along the lines of insertion of the myocommata 1 $c'c$, 2 $c'c$, 3 $c'c$, etc., this will serve to wrinkle the skin not only along the lines 1 $c'c$ 2 $c'c$, etc., but also to cause wrinkles to appear along the dotted lines, d, d', e and e'. In this way it is easy to see that the whole lateral integument will be thrown into definitely circumscribed rhomboidal areolæ in which separate overlapping scales s, s, s, s, may appear. The wrinkles thus produced by the

tension of myocommata upon the integuments of the body will cross
each other and be reinforced at six points in the zigzag transverse
course of each myocomma, viz., twice at each of the points c and c'
and along the line a, b, where the middle limb of the $\leqq$ rests.

The only point which now remains to be discussed is the imbrica-
tion of the scales. This is also as readily accounted for as the
delimitation of the scale-forming areolæ, s, s, s, and their tri-linear
arrangement in three directions in the convex surface of the integu-
ment by means of the mechanical hypothesis here outlined.   If we
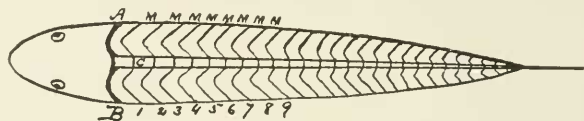

FIG. 2.

were to make a longitudinal transverse section through a fish along
the plane of the letters c, c, c, or c' c' c' of Fig. 1, we should get a
section like Fig. 2 in which the myotomes M, M, M, etc., Fig. 2
were again found to be V-shaped on either side of the medial axis
or vertebral column c, c, Fig. 2.   This proves that the myotomes
are really cones fitting into one another and that if we suppose the
first one to be inserted into the base of the skull along the line A,
B, Fig. 2, that point becomes the anterior fulcrum or *point d'appui*
of the whole muscular system.   The tensions thus developed upon
the skin along the successive myocommata 1, 2, 3 etc., Fig. 2, is
such that the integument would be flexed inward opposite each
myocomma as shown in the next figure, on a larger scale, which
represents the foldings of the integument at the surface of a part
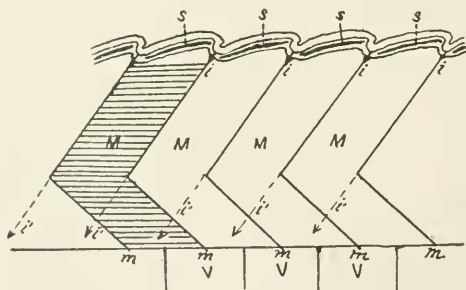of Fig. 2.   Here in Fig. 3, the myocommata m, i', m, i', m, etc.

FIG. 3.

are seen to be inserted
upon the internal face
of the epidermis ep, ep.
The membrane m, m,
m, m, acted upon by
the muscular fibres of
the myotomes M, M, M,
will have the effect of
pulling the integument
inward in the direction
of the arrows i', i', from

the linear points of attachment of the myocommata to the inte-

guments at *i, i, i,* toward the vertebral bodies V, V, V. In this manner will be developed the imbrication indicated by the heavy border along the posterior margins of the scales *s, s, s,* in Fig. 1, and in Fig. 3, in longitudinal section through the scale sacks or pockets at *s, s, s.*

It will be clear that in the case considered the arrangement and imbrication of the scales is determined by the actions of the segmentally arranged muscles of the body. In other words, whatever has determined the development of somites has also, in the most clear and direct manner, determined the segmentally recurrent and peculiar tri-linear and imbricated arrangement of the scales of many fishes. It may be urged in objection that heredity has determined the number, arrangement and the development of the somites and, therefore, the development of the scales is also a sequence of hereditary influences working thus indirectly. This view of the case may be admitted without invalidating the conclusion that, given the growing mechanism here described, the development of the scales would under any circumstances have been interfered with at the points where the integument was being continually flexed, wrinkled or folded as it is around the integumentary areolæ wherein the scales are formed, as has been here proved to correspond with the facts.

Special types of squamation amongst fishes may require an interpretation different as to details from the foregoing, but it is probable that such special cases will rather tend to confirm than otherwise the views developed in this sketch of an hypothesis respecting the mechanical origin of the arrangement and imbrication of the scales of fishes. For example, one of the most extreme cases, that of the sturgeon, shows that the smaller integumentary plates between the large dorsal, lateral and ventral rows, conform to these lines of tension of the myocommata upon the integument. An even more instructive example is that of the common eel in which the scales are oblong rhombs or parallelograms, arranged with their diameters in oblique lines, running in two directions conformably with the tensions, wrinklings and foldings of the integuments produced by the oblique insertions of the muscles when the latter are brought into action. Other cases where the scales are very fine might be urged in objection, especially where several oblique rows of scales are found to correspond to each somite. Such parallel duplication of scale rows, however, does not invalidate the principle since the rows

still conform to the lines of tension of the linear attachment of the myocommata to the integuments. The hypothesis may also be extended so as to consistently consider such forms as the pipe-fishes and other anomalous forms, where sluggish habits coupled with the almost exclusive use of the dorsal fin in swimming, has rendered the lateral musculature of the body comparatively subordinate in function, and which may even lead to secondary fusion of somites and the consolidation of consecutive pairs or triplets of vertebral centra into single vertebral bodies.

Two conclusions of prime importance may be drawn from the hypothesis and the evidence here presented, namely :

1. The scales of fishes bear a segmental relation to the remaining hard and soft parts, and are either repeated consecutively and in oblique rows corresponding to the number of segments, or they may be repeated in rows as multiples of the somites, or segmental reduction may occur which may affect the arrangement of the scales so as to reduce the number of rows below the number of somites indicated by the other soft and hard parts.

2. The peculiar manner of interdigitation of the muscular somites, as indicated by the sigmoid outline of the myocommata, as seen from their outer faces, and the oblique direction of the membranes separating the muscular cones, has developed a mode of insertion of the myocommata upon the corium which has thrown the integument into rhombic areolæ during muscular contraction. These areolæ are in line in three directions and the folds separating them, particularly at their posterior borders, are inflected in such a manner by muscular tensions, due to the arrangement of muscular cones, as to induce the condition of imbrication so characteristic of the squamation of many fishes.